THE GROWTH-FORMS OF NATAL PLANTS.

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(Communicated by Professor H. H. W. Pearson.)

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Contents.

INTRODUCTION.

The investigation of the growth-forms of plants in relation to their environment is being recognised as a very important, if not the most important, branch of Plant Ecology. The study of the various plant communities, and their determination by the environmental factors, presents a more general aspect of the subject, and has hitherto perhaps, on the whole, received more attention from plant ecologists, though, of course, it includes a certain amount of the study of the separate growth-forms. It is, however, in the more detailed study of the "epharmony" of the species of plants that a deeper insight is gained into the cause and effect relationship existing between the environment and plant life.

In its widest sense there is practically no branch of Botany that has not a direct bearing on this subject, since the aim of Botany is to explain why plants are as they are. There is a danger, therefore, in restricting oneself to a single line of inquiry, neglecting the others. For instance, Warming (23) points out that the influence of the environment on species is complicated by hereditary tendencies, of which the causes are not yet understood. One result of this is that different species adapt themselves to the same environment in widely different ways. To quote the example given by Warming: "While one species may adapt itself to a dry habitat by means of a dense coating of hairs, another may in the same circumstances produce not a single hair, but may elect to clothe itself with a sheet of wax, or to reduce its foliage and assume a succulent stem, or it may become ephemeral in its life-history." Warming is here obviously referring not to the environment as a whole, but to one main factor of the environment—in this case a "dry habitat." It may be doubted whether in Nature any two plants exist under absolutely identical environmental factors, though even if they did, they would not be identical in every respect, for it can hardly be supposed that the environments of any two species have remained identical throughout their evolution. If we had a full record of their past histories, we might be able to say why in reaction to dry conditions one species produces hairs, another wax, another reduces its foliage, and so on. It is hardly necessary to refer to "hereditary tendencies" until we have exhausted the possibilities. It is dangerous to lay stress on the reaction to one factor of the environment, neglecting the others, yet in most systems of classification of growth-forms this is what is done, and at the present state of our knowledge it is perhaps excusable. It is only to be expected, however, that species will be found reacting to that single factor when constant, in widely different ways, as in the example quoted from Warming.

On the other hand, different environmental factors may produce essentially the same growth-form. The effects of a dry atmosphere and "physiological drought," for example, may be the same, and when we take various combinations of external factors which differ among themselves, we often find more or less identical growth-forms resulting. The classification of growth-forms cannot, therefore, be based entirely on the adaptations resulting from definite and particular factors of the environment.

A further point which has been noted by the writer as being particularly true with regard to the growth-forms of Natal plants, is that many species are so very variable that they belong to more than one growth-form. Many lianes (*e.g. Scutia commersonii*) often grow as stout trees, yet lianes and trees form two of the six different main classes of growth-forms according to Warming's system of classification. In the same way certain species come into any one of the four subdivisions of phanerophytes, according to Raunkiaer's system (20, 22).

Such difficulties and limitations are, of course, sufficiently clearly recognised. We are a long way from the ultimate goal of a proper ecological interpretation of the various growth-forms. At present any investigation of the subject must follow certain lines.

The first essential is as thorough a knowledge as possible of the complete life-history (autecology) of each species. How very far we are from this ideal is being realised more and more clearly by all plant ecologists. In a recent paper (16) Prof. F. W. Oliver remarks: "Of the 120 species of flowering plants that form the known flora of Blakeney Point, it is doubtful whether we can truly assert that we are really familiar with the full life-histories of more than two or three." If this is true of a country like England, where there are so many workers, the difficulties confronting a single worker in a country like Natal can be better appreciated.

Of the habits of Natal plants and their full life histories, as studied in the field, really very little is known. Many of them are only known as herbarium specimens, and many more—in fact, the majority—have been named and described in the only available systematic work, *The Flora Capensis*, by botanists who have never seen them growing. It is not surprising, therefore, to find that growth-forms have received either very scant attention or none at all, or what is worse, incorrect information has been given. Apart from this, however, to a plant ecologist working in a new country, it is very useful to have some sort of a "Flora," or at least a list of species, to serve as a guide. Medley Wood's *List of Natal Plants* (26) is, therefore, of great assistance. Nor is it to be supposed that the *Flora Capensis* is in any way inferior to other similar works, in respect to the descriptions of growth-forms. As already remarked, "Growth-forms are too often very imperfectly described, even in the standard British floras" (22). Sim's *Forests and Forest Flora of the Cape of Good Hope* (21) contains much information regarding the growth-forms of the trees and shrubs.

The choice of a system of classification for growth-forms is a matter of the greatest difficulty. The guiding principle must be natural—*i.e.* the system must in itself show the dependence of the growth-forms on external factors—but the present state of our knowledge is such that any attempt at such a system must remain incomplete and unsatisfactory.

A short historical summary of the various systems that have been proposed is given in Warming's *Ecology of Plants*, ch. ii. The earliest is that of Humboldt (1805)—a purely physiognomic system, not founded on ecology (7, 8, 9). Grisebach (1872) put forward another physiognomic system, which he claimed, without good grounds, showed the influence of environment, particularly climate.

The systems of Drude (4), Krause (10), Pound and Clements (19), Raunkiaer (20), and Warming followed, all based on various ecological principles. It is unnecessary in this paper to repeat the summary of each given by Warming. The systems of Drude, Pound and Clements and

Raunkiaer agree more or less in emphasising the importance of the adaptations which enable plants to live through the adverse season. Warming's system is built on a broader foundation. He takes into account all the main adaptations and the main factors of the environment. His system shows a marked contrast to that of Raunkiaer, in that the latter chooses one main factor and to a large extent neglects the others.

Any worker who has to select a system will find that he must be guided by two principles :

1. Which system is most natural and scientific and interprets best the ecological facts.

2. Which system, under any given circumstances, can be applied most usefully.

As far as the first principle is concerned, in the writer's opinion, Warming's system is preferable to any of the others, though it, too, leaves much to be desired. But in attempting to apply it to the vegetation of Natal, the writer found that his knowledge of the facts was not sufficient to enable him to do so successfully.

Raunkiaer's system is much easier to use. It has been adopted by other Danish botanists, such as Ostenfeld (17) and Paulsen (18). An excellent account of it is given by W. G. Smith in the *Journal of Ecology*, vol. i, No. 1 (22). Not only is it easier to use, but it has the further advantage of lending itself to statistical and therefore comparative methods. The basis of the system is the nature and degree of protection possessed by the buds or shoot apices during the adverse season—*i.e.* in the case of Natal during the winter dry season. Raunkiaer has modified his system slightly since 1903. In a paper published in 1908 he adopts the following ten main classes of growth-forms or "life-forms":

1. S. = Stem-succulents.
2. E. = Epiphytes.
3. M.M. = Megaphanerophytes and Mesophanerophytes.
4. M. = Microphanerophytes.
5. N. = Nanophanerophytes.
6. Ch. = Chamaephytes.
7. H. = Hemicryptophytes.
8. G. = Geophytes.
9. H.H. = Helophytes and Hydrophytes.
10. Th. = Therophytes.

Phanerophytes are the trees and shrubs having their buds in the air. The buds may be naked or scaly, large or small. Phanerophytes may be deciduous or evergreen. Megaphanerophytes grow over 30 metres high (100 ft.). Mesophanerophytes, 8–30 metres (26–100 ft.). Microphanerophytes, 2–8 metres (6–26 ft.). Nanophanerophytes, less than 2 metres (6 ft.).

Chamaephytes include a variety of forms that have their shoot apices on the surface of the ground or not more than 25 centimetres (10 in.) above it. This does not mean that the plant during the vegetative season is not more than 25 centimetres high. The herbaceous parts may grow tall, but die down at the approach of winter. Small cushion forms and plants with long diageotropic shoots also come into this class.

Hemicryptophytes have their dormant shoot apices just below the surface of the soil during winter. The aerial parts die down. It is often very difficult to separate this class from the classes Chamaephytes and Geophytes. They naturally grade into one another.

Geophytes are plants with underground bulbs, rhizomes, and tubers of various kinds. The food material thus stored enables the renewal buds to be more deeply situated in the soil.

Helophytes are marsh plants which have their dormant buds at the bottom of the water or in the mud. Somewhat difficult often to separate from previous classes.

Hydrophytes are water-plants with winter buds or rhizomes.

Therophytes are annual plants—"plants of the favourable season." They live through the adverse season as seeds. In Natal it is not necessary to distinguish "summer" and "winter annuals."

Beginning with the Phanerophytes, those classes of growth-forms are arranged in a series showing increased protection against the unfavourable season. Phanerophytes are characteristic of favourable climatic conditions. Therophytes, if they predominate, show desert conditions.

In the following paper Raunkiaer's main scheme has been adhered to with very slight modifications, and consequently Raunkiaer's statistics and conclusions for other countries can be utilised for purposes of comparison. Where further subdivision was considered advisable, Raunkiaer has not been necessarily followed, seeing that Natal naturally differs from the countries in the Northern Hemisphere, to which Raunkiaer's papers refer.

MEGAPHANEROPHYTES.

Only slight reference need be made to this class, seeing that very few trees in Natal grow over 30 metres (100 ft.) high.

The Yellow-wood, *Podocarpus elongatus,* reaches a height of 120 ft. The other species, *Podocarpus thunbergii,* grows up to 100 ft. These are the dominant trees forming the upper canopy of the Yellow-wood Bush of Natal (1).

MESOPHANEROPHYTES.

These are the trees and lianes which grow over 8 metres (26 ft.). There are certain features, which belong more or less to the group as a whole. The buds are usually very small and not protected by conspicuous scales. In some cases, however, there are large stipules. The wood is usually hard and close-grained, and, in a great many species, of high specific gravity. The species are generally slow-growing. It is doubtful whether the rings in the wood are always, properly speaking, annual rings. A species may be in full growth at the end of summer, stop for a short time in mid-winter, begin again in spring, and stop for a short time in midsummer. This is certainly very noticeable in such trees as the Orange and *Pinus insignis,* as cultivated in Natal.

The total number of Mega-mesophanerophytes is *cir.* 95. A number of lianes of the ropy, woody type are included. They are the familiar "monkey-ropes" that are so abundant in the forests of Natal. The number included in the class Mesophanerophytes might easily be increased, but the others are included in the next class—Microphanerophytes—as being more often under than over 8 metres. In Warming's system the lianes are separated from the trees and shrubs—in fact, they form one of his six main classes of growth-forms. This is undoubtedly more natural, but as far as protection against the adverse season is concerned, there is no reason why they should be separated. By including them with the trees and shrubs we avoid a further difficulty in that many woody lianes, in the absence of support, grow as shrubs or small trees—*e.g. Scutia commersonii, Dalbergia obovata,* and others.

There are certain general features of the Mega-mesophanerophytes that may be summed up as follows:

(1) Great VARIATION IN SIZE AND FORM exhibited by the same species, depending on differences in the environment, particularly (*a*) the differences between Sand-dune Bush, other coast-bush, and inland-bush; (*b*) the differences between open Rocky Hillside, Thorn Veld, Stream Bush, and Close Bush. The details concerning each of those environments have been given by the writer in former papers (1, 2) and need not be repeated here. The point on which emphasis is desired to be laid is that many species in this class exhibit great plasticity or power of adaptability to widely differing environmental conditions.

The examples of lianes growing as trees and shrubs may be requoted, and, in addition, the following species illustrate this point:

Kiggelaria africana, Toddalia lanceolata, Ekebergia capensis, Trichilia emetica, Apodytes dimidiata, Pteroxylon utile, Rhus laevigata, Schotia latifolia, Milletia caffra, Albizzia fastigiata, Plectronia obovata, Nuxia congesta, Myrsine melanophleus, Cordia caffra, Celtis kraussiana, Ficus capensis.

(2) VARIATION IN FOLIAGE of the same species depending on the same differences in environment as the last. The leaves of certain species are more succulent nearer the coast. The leaves of others are larger nearer the coast, or the shape of the leaf may change from the coast, inland. There is variation also, according to whether the tree grows isolated (Thorn Veld, Rocky Hillside), semi-isolated (Stream Bush), or in dense forest.

Examples: *Scolopia zeyheri, Kiggelaria africana, Calodendron capense, Xanthoxylon capense, Ekebergia capensis, Ilex capensis, Celastrus peduncularis, Nuxia congesta, Apodytes dimidiata, Cussonia spicata.*

(3) The DEGREE OF PUBESCENCE varies greatly in the same species and in different species.

(4) A DECIDUOUS TENDENCY is seen in *Commiphora caryaefolia, Schmidelia melanocarpa, Bersama tysoniana, Albizzia fastigiata, Celtis kraussiana, Zizyphus mucronata, Pteroxylon utile, Rhus laevigata, Plectronia mundii, Rauwolfia natalensis, Croton sylvaticus,* some of which are almost always wholly deciduous, others being irregularly deciduous or semi-deciduous. The deciduous tendency is more pronounced inland and at higher altitudes than on the coast, as shown by the species, *Erythrina caffra, Calodendron capense, Cordia caffra, Celtis kraussiana,* which are deciduous inland, but usually more or less evergreen on the coast.

Some species are evergreen, or semi-deciduous or deciduous, according to locality and general environment, apart from proximity to the coast, *e.g. Trimeria alnifolia, Ekebergia capensis, Elaeodendron croceum, Plectronia mundii.* Altogether, about 20 per cent. of the species show the deciduous tendency to a greater or less extent—a reaction to the adverse environment of the dry winter season.

(5) SPINOSITY.—The majority of the thorn trees of the Thorn Veld, etc., belong to the next class, Microphanerophytes, and the whole question of thorn development will be discussed more fully when that group is dealt with. Some of the Acacia species with thorns, though included in the next class, occasionally exceed 8 metres in height. Several of the taller trees included in the above list show a variable amount of thorn development, *e.g. Scolopia zeyheri, Xanthoxylon thunbergii, Zizyphus mucronata, Scutia commersonii, Erythrina caffra.*

(6) A THICK BARK is a feature of a considerable number. It is particularly noticeable where the species grow in such situations that they are exposed to grass fires, and it doubtless acts as a protection. The following species show it:

Apodytes dimidiata, Trichilia emetica, Bersama tysoniana, Albizzia fastigiata, Odina caffra, Pygeum africanum, Cunonia capensis, Eugenia cordata, Cussonia spicata, Cussonia umbellifera, Curtisia faginea, Plectronia obovata, Myrsine melanophleus, Sideroxylon inerme, Olea foveolata, Olea laurifolia, Rauwolfia natalensis, Commiphora caryaefolia, Ocotea bullata.

The same feature is characteristic of many included among Microphanerophytes.

(7) A FREE DEVELOPMENT OF COPPICE SHOOTS often modifies the original growth-form considerably, giving the appearance of an abnormally large trunk, or the main stem may die away and become replaced by a cluster of coppice stems.

Examples: *Xymalos monospora, Ocotea bullata, Kiggelaria africana, Rhus laevigata, Milletia caffra, Milletia sutherlandi, Nuxia congesta.*

(8) The EFFECT OF EXPOSURE, particularly along the seashore, in causing branching from the base, is seen in *Sideroxylon inerme, Mimusops caffra,* and others.

Taken as a whole, the class of Mesophanerophytes show certain progressive adaptations to unfavourable conditions, of which the most important are, decrease in size (which is often very marked), increase in succulence and other xerophytic characters in the foliage, increase of pubescence, a tendency towards becoming deciduous, increased branching from the base and formation of coppice shoots, which often replace the main stem, a development of thick bark, and spinosity.

Not only are those features and tendencies illustrated by the species making up the whole class, but also by the individuals of single species, often in a most striking manner. Among unfavourable conditions we must include not only the adverse conditions of the winter dry season, but also exposure, proximity to the sea, and other factors which serve to differentiate the various habitats at all seasons of the year.

While we use the degree of protection of the buds or resting shoot apices as the main character serving to determine the class as a whole, we are able to use any of the other features mentioned to serve as a basis for further subdivision. For instance, we might choose the somewhat artificial distinction of thickness in the bark, and arrange the species in a series accordingly. Or we might form subgroups as follows: Evergreen, semi-deciduous, deciduous.

Whatever system of subdivision might be adopted, the variability of single species would be found very troublesome, and the class, as a whole, is not so large that any subdivision is necessary. At the same time, it is necessary to notice as clearly as possible the various tendencies exhibited by the class. This must be our excuse for presenting them in tabulated form above.

MICROPHANEROPHYTES.

It will be obvious that no sharp line of distinction can be drawn between any of the groups of Phanerophytes or other classes of growth-forms. Such forms as *Celtis kraussiana* or *Myrsine melanophleus* might be classed as Nano-, Micro-, or Mesophanerophytes, according to circumstances. Many of those included in the list of Mesophanerophytes only occasionally reach the necessary dimensions. On the other hand, a few of those included among Microphanerophytes sometimes exceed 8 metres (26 ft.) in height. There are numerous instances, again, of the same species assuming different growth-forms—shrub, tree, or woody liane, *e.g. Dalbergia obovata.* In fact, this great variability in the same species, as will be illustrated throughout this paper, is one of the most striking features of Natal vegetation, and it cannot be too much emphasised. It is due, doubtless, in the first instance, to the very great range of differences in the natural conditions, and it proves also that the native plants of Natal possess great plasticity, in that single species are thus able to adapt themselves to very distinct environments.

The total number of Mesophanerophytes is *cir.* 420. The main features to be noted of this group are :

(1) Proportion of Lianes.—Over 30 per cent. of the Mesophanerophytes of Natal are climbers. Certain large genera, such as *Vitis* and *Ipomaea*, with sixteen species in each, help to swell the number. A notable feature is the number of shrubby species, which, in the absence of support, grow erect and may even form small trees, yet under suitable conditions become scandent. Almost every known variety of liane is found (except root-climbers).

Some are simple scramblers, with the usual elongated type of stem, but with none of their organs specially modified for climbing ; others possess various kinds of tendrils. Many are spiny. Some are semi-herbaceous perennials—the annuals are, of course, not included here—but the majority are of a woody type.

The watch-spring tendrils of the woody Dalbergias, etc., are well known. The various stout lianes of the forest are popularly known as "Monkey Ropes." They form dense festoons and masses, and make it somewhat difficult to penetrate through the bush. They are particularly abundant in the Sand-dune Bush of the coast, in which there is little other undergrowth. From the economic standpoint, those "monkey ropes" must be ranked as the most pernicious weeds of the forest, since they often smother and kill the trees over which they climb. Their presence in such abundance alters the ecological character of the bush as a whole. They fill in the gaps, so that very little light penetrates, and the undergrowth of shrubs and herbs is very scanty, being confined more or less to the margin of the bush. The lianes also influence the regrowth of the forest. In the denser shade produced by them, the seedlings of light-demanding trees are killed, so that these also are confined to the outside margin of the bush.

An increase in the number of lianes, therefore, leads to a decrease in the number of Nanophanerophytes and Chamaephytes, etc., inside the bush, and the lianes also modify the growth-forms and influence the distribution of the Mesophanerophytes. No better instance could be found of the vegetation itself as a factor influencing the vegetation. The dependence of the lianes themselves on the phanerophytes (trees) over which they climb is, of course, still more obvious.

(2) Variation in the Growth-forms of the separate Species.—This follows more or less the same lines as the Mesophanerophytes. The great plasticity of certain species is again noticeable. The size, amount of

branching, general form, shape and size and structure of the leaves, degree of succulence and pubescence, all vary according to whether the species grows isolated or in the bush, and according to the plant formation of which it forms a part—Bush, Stream Bush, Sand-dune Bush, Rocky Hillside, or Thorn Veld. A much-branched shrub, given suitable conditions, may develop as a small tree. This is what is to be expected, and hardly calls for further remark. The tendency of shrubs to become lianes, as already mentioned, is more noteworthy.

(3) The DECIDUOUS TENDENCY is not perhaps quite so well marked as in the case of Mesophanerophytes. The species that show it are deciduous or evergreen, according to circumstances, *e.g. Dombeya dregeana, Ehretia hottentottica, Rhus spp., Excoecaria africana, Excoecaria reticulata, Erythrina tomentosa, Acacia spp.*

(4) As a result, partly perhaps of grass fires, THICK BARK is a feature of most of the species that grow isolated or semi-isolated in the thorn veld, on rocky hillsides, or on the outer margin of the bush.

Another effect of grass fires is seen in Microphanerophytes and also in Nanophanerophytes. Many shrubs and even small trees in similar situations (veld and outer margin of bush) are constantly burned down to the ground. The result is that there is a succession of annual shoots from a permanent root crown.

(5) INFLUENCE OF FROSTS.—On the coast belt, frosts are practically unknown, and many species grow there which are not found at the higher altitudes inland. The growth-forms of other species differ in the two regions (coast and inland) owing to the fact that in the latter they have to endure frosts. The upper shoots die off, and the result is as if the shrub had been pruned back. New shoots quickly develop in spring, and we thus get a succession of annual branches from a certain height. This effect is therefore similar to that of fires, but it is not so drastic. The difference in growth-form depending on this factor may be seen not only in comparing coast plants with those inland, but also among the inland plants themselves. In the Midlands there are many localities where frosts are rare, *e.g.* sheltered side valleys opening out into a deeper main valley where the cold air is drained off. Also the higher ridges and hills, where the gradient is sufficient to allow of rapid cold-air drainage, do not suffer so much as the main valleys. In such places species are not so much affected by frosts.

(6) SPINOSITY.—The question of the cause of thorn development is one that has of recent years given rise to a good deal of discussion, and it cannot be said, as yet, to have been satisfactorily answered.

A. Lothelier (1890–93) published the result of researches on *Ulex europaeus, Berberis, Crataegus,* etc., in which he showed that dryness of the atmosphere and intense illumination favoured thorn production. He found that in moist air, or in feeble light, branches which normally developed as spines became leafy shoots.

Cockayne found the same in the case of *Discaria toumatou* and supported Lothelier's view.

Zeidler (1911) opposed Lothelier's views. He found that under moist conditions and in feeble light thorns were developed in *Ulex*, and he regarded the leafy shoots obtained by Lothelier as being juvenile forms, the thorny shoots being the adult.

In his reply to Zeidler's criticism, Lothelier (1912) defends his former position, and states that if the leafy shoots are produced only in moist air the latter must be considered as the cause of their production; and if Zeidler's view is correct, the leafy "juvenile" form ought to become spiny towards the growing end. This, however, is not so.*

MacDougall (1912) tested the actual behaviour of the spines of *Echinocactus* with regard to atmospheric moisture. He found that they were hygroscopic, and could take up and lose water "as any bit of dry wood might do it," but he concluded that the resulting changes in weight of *Echinocactus*, due directly to humidity, do not affect the succulence of the living tissues. So that even if we accept Lothelier's views that spines are caused by intense illumination and vigorous transpiration, it is not yet clear what their exact physiological significance is or how the plant benefits, if it benefit at all.

Another view not necessarily entirely opposed to the above is that thorns serve to protect plants against animals. Very little positive evidence can be brought forward in support of this view, and the hypothesis is in the main a purely teleological one. As Warming points out, "it is evident that spiny plants, by reason of their armed nature, may defeat unarmed species, and become more widely distributed, but for all this we are not entitled to assume that thorns are a *direct* adaptation to animals, or that they arise in a country rich in herbivorous animals." In Arctic countries, however, there are large herds of large, herbivorous animals—*e.g.* reindeer and musk-ox—yet there are no thorns, because the conditions of humidity are not suitable for their production.

The only way in which the question of the function of thorns is likely to be cleared up is by controlled experiments, preferably carried out in the field, but certain facts may be noted concerning the thorny species of Natal as follows:

(*a*) The majority of the thorny species grow in dry situations—*e.g.* the thorn veld, sand-dunes, rocky places. Of these the various species of *Acacia* are typical.

(*b*) On the other hand, certain species that grow in the Close Bush under

* For a review and abstract of Lothelier's 1912 paper, see Journal of Ecology, i, 2, p. 123.

moist conditions are thorny also—*e.g. Xanthoxylon capense, Scolopia zeyheri*, and various lianes. In the case of the latter the thorns may be considered as organs modified to assist in climbing, though it is doubtful whether this explanation applies in all cases.

(*c*) Certain of the more accommodating species occur both in the Close Bush and also in the dry Thorn Veld. In such cases there is usually a much greater development of thorns in the latter. Sometimes a species may be thornless in the Close Bush and possess long spines in the Thorn Veld—*e.g. Celastrus buxifolius.*

(*d*) In the same way species are sometimes more thorny on the sand-dunes than elsewhere. In other cases, however, the foliage is more succulent in this situation and less prickly—*e.g. Xanthoxylon capense.* It is worthy of note that *Scolopia zeyheri*, according to Sim (21), is usually thornless on the sand-dunes.

(*e*) Though in the individual species increased thorn development with increased aridity is the rule, there is often a certain variability in thorn development which does not seem to depend on that factor or on more intense illumination. Young plants of Acacia are sometimes—in fact, one might say as a rule—very thorny, and become less so as they grow. A passing reference may be made here again to Zeidler's theory. He supposed that leafy shoots of Ulex are "juvenile"; thorny shoots "adult." The Natal Acacias show exactly the opposite phenomenon. Juvenile plants are very thorny indeed; adult ones less so. Frequently there is a large thorn development on coppice shoots. These alone may be thorny and the rest of the tree unarmed, as *e.g.* in *Plectronia mundii, P. pauciflora, Aberia tristis*, etc.; or the spines in the coppice shoots may be more abundant and much larger than those on other parts of the tree.

Aberia caffra is often thornless in the tree form, but very thorny if kept cut as a hedge. Marloth is quoted by Warming (23) as having called attention "to specialised adaptation exhibited by certain species, in that the longest and strongest spines occur on young individuals or on root shoots which are most accessible to animals, while the branches subsequently produced on tall trees are quite devoid of spines." Warming further adduces the case of *Ilex aquifolium*, the upper leaves of which are usually not prickly when once the plant has grown into a tree.

Here, then, we seem to have certain facts which support the "protection against animals" theory. But like many other cases, where a theory has to be supported simply by observed facts in Nature and not by controlled experiments, the amount of support given to the theory depends largely on how the facts are presented. In the case under discussion, certain other facts must be considered, to reach a fair conclusion. In the various Acacias, the dominant trees of the Thorn Veld, there is a considerable variation in growth-form, as well as in degree of spinosity. The "umbrella" form is most typical—a short bole and a wide-spreading crown—a growth-form adopted in relation to the dry, hot winds, to which the trees are fully exposed. This umbrella form is brought about by slow, regular growth, with branching at the apex. The lower branches are the oldest, and are not the result of vigorous branch development from dormant buds. In such cases those lower branches are often destitute of spines and are covered with lichens. This umbrella form is typically a more leafy form, and has fewer and smaller spines than other forms. Leaf development and spine development, as is well known, usually vary inversely.

In other cases, the species of Acacia show more upright, irregularly branched, straggling growth, due largely to more vigorous development. Lower branch buds in these forms frequently develop rapidly, forming the so-called "gourmand" shoots. On such branches, spines are larger and stronger. *It is not therefore a case of the lower branches as such showing a greater degree of spinosity, but branches that are growing more vigorously.* This applies also to young plants and coppice shoots and to *Aberia caffra*, when kept as a hedge.

On the other hand, in such a case as *Scolopia zeyheri*, the spines (which may be absent altogether) are often absent from the crown and present on the main trunk 6–8 in. long. Here it is the older part of the tree, which is armed. But it is difficult in this case to see what protection this affords to the foliage of the tree.

The evidence, in the main, seems to support Lothelier's view, that spine development is the result of dry conditions and intense illumination. The thorny species which occur in the Close Bush do not disprove Lothelier's view, for, as is pointed out elsewhere (1, 2), the Close Bush of Natal has certain xerophytic characters, and is, in fact, intermediate between sclerophyllous woodland and tropical rain forest. The foliage of many of the Close Bush trees is of a distinctly xerophytic type, *e.g.* that of *Podocarpus*, the dominant tree of the Yellow-wood Bush. It is not surprising, therefore, to find some of the species in the Close Bush also possessing thorns. With drier conditions the spinosity undoubtedly increases, and that in a most striking manner, until it culminates in the vegetation of the Thorn Veld and dry, rocky hillsides of the Low Veld region. The production of thorns may then be looked upon as one of the visible results of the process of lignification, which is characteristic of xerophytes, the physiological significance of which is still somewhat obscure, but which the researches of Lothelier, as well as the evidence presented by the growth-forms and distribution of the species of plants concerned, have shown to be favoured by dryness of the atmosphere and intense illumination.

Accepting this, we may still ask whether, being produced in this way, they may not then serve as a protection against animals. This is a very different position from supposing that thorns have been *evolved* as a protection against animals. It is not necessary to suppose that in all cases they do so serve, and, as a matter of fact, if we did attempt to show that the producing of thorns is a method adopted by the plant to defend itself, all that can be said is that, in certain cases, the plant has shown itself singularly maladroit, protecting parts that do not seem to need protection, and leaving other important parts—its crown and foliage generally—unprotected, *e.g.* *Scolopia zeyheri.*

The palm, *Phoenix reclinata,* calls for special mention. The leaves are 4–8 ft. long, with the lower pinnae reduced to sharp spines. These surround the crown of the stem, which contains a sugary sap. The possession of spines by palms, especially those inhabiting the Amazonian forests (*Astrocaryum* and *Bactris*) is certainly somewhat difficult to explain by Lothelier's theory (23).

As Warming also points out, "In the north, temperate, moist climate, there occur many thorny growths, the significance of which is at present obscure." Indeed, it must be admitted that there is much in the whole subject that remains at present obscure, and it has been the writer's object to bring forward the facts as far as Natal plants are concerned, and not at present to attempt to argue strongly for one view or the other, though, as already stated, in his opinion, the facts in the main support the views of Lothelier, Cockayne, and others—views that agree in supposing that thorn development is a reaction to dryness of the atmosphere.

NANOPHANEROPHYTES.

The determination of the growth-forms belonging to this and the following two classes has been a matter of much greater difficulty than the preceding. The actual height of the plant does not serve as a guide, for if it be a herbaceous or suffruticose form it may or may not die down in winter. The information given in the *Flora Capensis* is, therefore, of little use. At the present state of our knowledge, and dealing with such a country as Natal, it is impossible for anyone to give details regarding the life-history of each species. A knowledge of the habitats is of great assistance. It is safe to assume that typical veld plants either die down or get burned down to the ground in winter. Since the class of Geophytes (bulbous plants, etc.) is a fairly definite one, where any doubt exists, it lies between the classes—Hemicryptophytes and Chamaephytes. Doubtless mistakes have been made in the enumeration, but it is hoped that these will to a certain extent neutralise one another, so that the percentages will not be affected; nor is it likely they will be, since we are dealing with such large numbers. Species growing inside the bush or in other situations where they are not affected by fire, though they may be herbaceous or very weakly lignified, commonly persist through the winter, and even continue their growth, *e.g.* species of

Acanthaceae. Among the most troublesome are those forms (the Labiate type of undershrub of Warming) where considerable parts of the flowering shoots die after blossoming. Since one is naturally acquainted more with the appearance of the plant at the time when it flowers, one is often inclined to put it down as Nanophanerophyte when it ought to be classed as Chamaephyte.

The total number of Nanophanerophytes is *cir.* 430. They form a somewhat heterogeneous class, much more so than any of the preceding classes. This being the case, some further subdivision is possible, and such subdivision can follow various lines.

As is well known to all botanists, certain large families of flowering plants have a striking similarity in their vegetative parts, so much so that it is often possible to tell at a glance to what family a plant belongs, without examining the flowers. Taking advantage of this fact, we might pick out certain types of growth-form from this class and name each after the natural order, of which it is most characteristic.

Such a simple scheme of subdivision is one that readily suggests itself. The earliest writer on growth-forms, *Humboldt* (1805), adopted it. He treated in detail the forms of the palm, banana, malvaceous and bombaceous plants, mimosa, heath, cactus, orchid, casuarina, conifer, pothos, liane, aloe, grass, fern, lily, willow, myrtle, melastomaceous plant, laurel.

Though it is interesting enough to recognise such "family resemblances" in growth-forms, yet if we attempt to push it very far it has really very little scientific value, as the scheme is not based on ecological facts. The members of no family of plants all belong to the same growth-form, and after we have removed the forms belonging to each of the types mentioned above, or to any similar collection of types, we are left with a still more heterogeneous collection, to which we have been unable to assign places in any of the types. Not only, therefore, is such a scheme not based on ecological facts, but it is not exhaustive. It is simply a somewhat superficial recognition of certain resemblances in the vegetative organs of plants without any reference to any underlying principle or explanation.

The attempt to apply it generally, as Humboldt did, to the whole of the flowering plants must necessarily fail. At the same time, there is much that is attractive about the system of nomenclature. It can be made quite scientific if we adopt some definite ecological factor as a basis for the scheme, and it can be applied successfully provided we are dealing with one definite ecological group, such as the Nanophanerophytes. In other words, though it cannot successfully be applied as a basis for the main ecological divisions, yet it can be used in minor subdivisions. There is little likelihood of any confusion arising from introducing systematic names into ecology. No one, for instance, is likely to suppose that when we speak of "Heath form" or "Acanthaceous form" we restrict ourselves to Ericaceae and

Acanthaceae respectively. The ecological factor selected as a basis is the degree of lignification and xeromorphy. Thus we can arrange the Nanophanerophytes in a series, showing increased amount of lignification and xeromorphy according to variation in the environment, as follows :

(1) Soft-stemmed herbaceous perennials, with persistent aerial parts, *e.g. Phytolacca spp.* These are somewhat rare as Nanophanerophytes, but abundant as Chamaephytes (*vide infra*).

(2) Acanthaceous Type.—Weakly lignified undershrubs with thin leaves. They are commonly shade-loving bush plants, growing in the more open parts of the bush, or around the bush margin in a moist habitat. Many of them flower in winter, *e.g.* various species of Acanthaceae, Verbenaceae, Labiatae, *Piper capense*, etc.

(3) Leguminous Type.—Woody, much-branched shrubs, more characteristic of open spaces and veld, and often reduced to Chamaephytes by grass fires.

(4) Composite Type.—Shrubby Compositae, etc., often growing rather tall, but having various xerophytic modifications, such as thick leaves (*Osteospermum*), dense coating of hairs, etc., particularly abundant on the Drakensberg at high altitudes.

(5) Ericaceous Type (or Heath Type).—Almost too well known to require further description. It includes the Ericaceae (eighteen species) as well as isolated forms, occurring in widely separated families. Rosaceae (*Cliffortia*), Thymeliaceae (*Passerina, Lasiosiphon*)—another Alpine type.

(6) Succulent Type.—Fleshy plants, with persistent aerial parts over 25 cm. tall—Aloes and certain Crassulaceae.

(7) Lianes.—Species of Asclepiadaceae, etc., many of which are also Geophytes. The lianes, as in all the other classes, form a group by themselves.

The number of intermediate types might be multiplied considerably, but it is hardly necessary to do so. Every gradation in xeromorphy is naturally shown within the limits of a large class, such as the Nanophanerophytes. The types mentioned above simply mark certain definite stages.

We have now dealt with all the Phanerophytes, and, considering the group as a whole, we notice a progressive tendency towards greater protection during the adverse season. This is shown by a decrease in size, and this simple fact has been selected by Raunkiaer as a basis for his divisions. Further, it is noticeable that Mesophanerophytes tend to be reduced to Nanophanerophytes, and these in turn to Chamaephytes.

It may be remarked here that mere size or rather height is not, in all respects, a very satisfactory basis for classification. It is quite true that, taking into account only the inorganic factors of the environment, a taller plant is less protected than a shorter one, other features being equal. But where plants grow in such intimate relationship to one another, as they do in the bush for example, one plant affects another and the non-living environment is highly modified. The result is that the same species varies very greatly, according to whether it grows gregariously in the bush or isolated outside the bush. This presupposes, of course, that the species is sufficiently accommodating to do so, but the examples of trees and shrubs which are of this nature are very numerous in Natal.

However, this difficulty would arise, no matter what basis for subdivision were selected. Raunkiaer's system, as a whole, endeavours to arrange growth-forms in a definite series, showing increased protection to the growing apices during the adverse season. The Nanophanerophytes are supposed to show greater protection than the Microphanerophytes. In the main this is the case, yet we find Microphanerophytes—*e.g. Acacia spp.* and numerous other trees—fully exposed to the dry, hot winds, and extremely adverse environment of the Thorn Veld ; while Nanophanerophytes—*e.g.* species of *Justicia* and other Acanthaceae, *Piper capense*, etc.—occupy the sheltered, moist environment of the Bush. Here, then, are members of a class, which, according to Raunkiaer's scheme, ought to show greater protection, occupying a habitat where such greater protection is not required.

As a matter of fact, except in height, such species do *not* show greater protection. Most of them are distinctly mesophytic. The difficulty arises again from the choice of a single factor as a basis for classification. By choosing height as the basis for subdividing the Phanerophytes, Raunkiaer certainly gained by making his system very easy to apply. In temperate regions, where the forests in winter do not afford the same protection to the undergrowth and where frost and snow have to be taken into consideration, the height of a species is a more certain guide than in a subtropical country like Natal, and shows a truer ecological relationship. But in all countries, and especially in countries with evergreen forest, the height of species must remain a somewhat artificial basis for classification.

The dominant trees of the forest are certainly taller than the trees of the Thorn Veld, the latter thereby showing reaction to more adverse conditions, but the undergrowth of the forest enjoys a more favourable environment than the trees that afford it a protection ; yet the undergrowth cannot from the nature of things obviously grow taller. It is not necessary to labour the point. Enough has been said to show that Raunkiaer's scheme does not in its details show strictly the reaction to the adverse season. At the same time, it is difficult to improve it without detracting from its chief merit—the ease with which it can be applied. There does not seem to be any other single character that would suit better than height as a basis for the subdivision of the Phanerophytes.

CHAMAEPHYTES.

This class includes all the forms which lie on the surface of the ground during winter or have their shoot-apices not more than 25 cm. above it. The next class, Hemicryptophyte, is also a large one, and as the two grade into each other, it is not an easy matter to separate them. As a result of the tendency mentioned above, the Chamaephytes of Natal have been increased at the expense of the Phanerophytes, and are much more numerous than in the world's flora as a whole (the normal spectrum of Raunkiaer).

Among Chamaephytes, Raunkiaer distinguished four sub-types as exemplified by the European flora.

(1) Active Chamaephytes, with shoots diageotropic and persistent throughout their whole length—*Empetrum nigrum*, *Lysimachia nummularia*, etc.

(2) Passive Chamaephytes, with weak stems which lie on the ground—*Stellaria holostea*, *Cerastium trigynum*, etc.

(3) Suffruticose Chamaephytes, in which the herbaceous parts die down—species of Labiatae, Papilionaceae, etc.

(4) Cushion Plants.

All four sub-types are well represented in Natal, as well as certain others.

The total number of Chamaephytes (excluding Pteridophyta) is *cir.* 570.

The four types of Chamaephytes distinguished by Raunkiaer are well represented in Natal, and in addition there are other types which do not fit well into any of Raunkiaer's. As in the case of Nanophanerophytes, we can arrange the Chamaephytes in a fairly definite series, showing progressive adaptation to more rigorous conditions, as follows:

(1) Streptocarpus Type.—There are sixteen species of Streptocarpus in Natal. They are found usually in damp situations, near streams in the bush. The peculiar growth-form, with its single, permanent cotyledon which slowly increases in size, is quite distinctive and unlike anything else.

(2) Herbaceous Chamaephytes.—There are numerous species which have herbaceous but persistent aerial portions, *e.g.* species of *Geranium*, *Pelargonium*, *Lobelia*, *Wahlenbergia*, etc. They continue their vegetative work right through the winter, though not in most cases actively. They vary according to situation. If growing in a dry or exposed place, a species may die down to the ground, yet the new growth commences just above the soil. Such forms—*e.g.* many grasses—come very near the Hemicryptophytes.

Other examples of this type of herbaceous Chamaephytes, when growing in unfavourable situations, become annuals, *e.g.* *Hebenstreitia spp.*, *Polygonum spp.*, *Chenopodium spp.*, and many grasses. This is quite common. In fact, the majority flower and seed in their first year, so that they are not dependent on vegetative existence during winter. In certain situations, and in particular in cultivated soil, they are always annuals.

(3) Passive Chamaephytes, as defined by Raunkiaer, are weak-stemmed Chamaephytes, which lie on the ground. They ought, perhaps, to be included in the last class. There are numerous examples similar to those quoted by Raunkiaer, *e.g.* species of Caryophyllaceae and Ficoideae, *Alysicarpus rugosus, Cyathula sp., Amarantus sp.*, Cucurbitaceae.

Herbaceous and passive Chamaephytes are particularly abundant around the foot of spreading thorn-trees, and among clumps of them in the Thorn Veld.

(4) Cushion Plants, *e.g.* species of *Muraltia, Selago, Helichrysum*, etc.—characteristic of the higher altitudes.

(5) Active Chamaephytes.—Shoots diageotropic and persistent—species of Leguminoseae, *Oligomeris dregeana, Monsonia ovata*, species of Malvaceae.

It is rare to find these persistent through their whole length. They usually die back more or less, the extent to which they do so depending on situation. Often, as in other types, they die back and leave a small root-crown above the ground.

(6) Fleshy-leaved Chamaephytes are rather numerous in Natal, mostly species of Crassulaceae and *Mesembryanthemum.* Many of the Crassulaceae are rosette forms. The older leaves die off in winter.

(7) Suffruticose Chamaephytes.—These all die back considerably in winter, *e.g.* species of Labiatae (the Labiate type of Warming), Leguminoseae, Compositae, Rubiaceae, Verbenaceae, Selagineae, etc. The commonest type of all in Natal.

(8) Forms which invariably die down so far that they are almost Hemicryptophytes. All the Chamaephytic grasses, except one or two, such as *Arundinaria tesselata*, "the Berg Bamboo," are of this type. Since the two classes (Ch. and H.) grade into each other, there are naturally many intermediate forms. Perhaps too many of these have been included as Chamaephytes, but apart from the doubtful species the class is undoubtedly a very large one in Natal—a fact which requires some explanation. As a result of his careful analyses of various floras in the Northern Hemisphere, Raunkiaer found that Chamaephytes increased northwards in the Arctic region, and are particularly characteristic of the circumpolar regions, where, during the adverse season, a covering of snow helps to protect them. They also increase in warm regions which have a dry season. Raunkiaer's figures show a high percentage for Aden and the Libyan Desert.

The Hemicryptophytes are characteristic of the cold temperate regions, where there is sufficient precipitation, but where there are severe winter frosts without a constant covering of snow.

The Phanerophytes are most abundant in warm regions with uniform temperature and large rainfall.

In Natal we have practically no snow—on the coast belt not even frost. The frosts are nowhere very severe, the soil rarely being frozen. The winters in Natal are, however, very dry, and there are occasional hot winds, which add greatly to the dessicating effect. Phanerophytes are confined to the sheltered places, where the rainfall and mists are greatest—the southern and south-eastern slopes of the hills and edges of the terrace plateaux—except in the case of the trees and shrubs of the Thorn Veld—a very xerophytic type. The dryness of the winters, therefore, combined with the hot winds, deprive Natal of a Phanerophytic climate.

The absence of severe frosts and the dry winters again make the climate of Natal not a Hemicryptophytic one. The high percentage of Chamaephytes may, therefore, be put down as being caused by the dryness of the winters, combined with the absence of severe frosts and intensified by occasional hot winds. Natal can then be compared with places like Aden and the Libyan Desert. We shall find, however, that there are important respects in which Natal differs from those places. The percentage of Chamaephytes is about the same, but the percentage of Therophytes (Annuals) is very much less for Natal—in fact, it is abnormally low. This point will be discussed more fully later on, but it is mentioned now because one feels constrained to pause and ask whether the above explanation of the high percentage of Chamaephytes is the only one, and sufficient in the case of Natal.

The Chamaephytic growth-form, reduced as it is to within 25 cm. of the ground during winter, is well adapted to withstanding drought. The shoot apices are often protected by the older parts, which have died away, and so have formed a certain amount of *débris*. Phanerophytes, as we have seen, tend to become reduced to Chamaephytes by the adverse environmental factors. But among Chamaephytes we have included sixteen species of *Streptocarpus*, and many soft-stemmed herbaceous plants. These are not adapted to withstanding our adverse winter conditions. They do so successfully, because a moist, protected habitat is supplied to them by the Phanerophytes that compose the bush.

Take away the Phanerophytes, and the bulk of those species of Chamaephytes would disappear also. Stress ought to be laid on this fact, for to a certain extent it contradicts the view that an increase in the number of Chamaephytes indicates the influence of drought in warm countries. Even some of the more xerophytic Chamaephytes are found usually below the thorn trees of the Thorn Veld. Such facts illustrate once more the complexity of the whole problem, especially with regard to the influence of one type of growth-form on the others.

HEMICRYPTOPHYTES.

The aerial portions here are wholly herbaceous and die away at the approach of winter, leaving dormant shoot apices just below the surface of the soil. The difficulty of separating this class from the preceding one has already been sufficiently emphasised.

The total number of Hemicryptophytes is *cir.* 540. It is noteworthy that out of this number about 200 belong to the Compositae (including a large number of rosette and half-rosette forms), 100 to the Gramineae, and about 40 to the Cyperaceae. With regard to the latter, it should be noted that in the wetter parts of the veld we have grasses and sedges, also characteristic of the vleis, and it is not easy to determine which belong to the Hemicryptophytes and which to the Helophytes.

The Hemicryptophyte class, as a whole, is much more homogeneous than the last one, and there is therefore less need of subdivision. The rosette or half-rosette form is common.

In colder countries, where the Phanerophytes are mostly deciduous, the Hemicryptophyte class includes a large number of woodland plants. These are not abundant in Natal. There is not very much undergrowth, except around the edge of the bush, and what there is consists mostly of Nanophanerophytes and Chamaephytes, especially the Acanthaceous type of the former.

The Natal Hemicryptophytes are mostly veld plants, but, as pointed out in former papers (1, 2), the veld of Natal has several ecological features similar to deciduous woods—*i.e.* as regards the associated plants. The fall of the leaves from the trees in the one case, and the burning of the grass in the other, exposes the ground during winter. Herbaceous plants, in both cases, lose their aerial parts. In spring they grow quickly, and a great many of them get their flowering over before the leaves appear on the trees or the grass grows tall enough to shade them. The next class, Geophytes, are similar in this respect, and further reference will be made to the question when these are dealt with.

Another question dealt with at considerable length in former papers by the writer (1, 2) is that of changes in the veld due to the influence of man, both direct and indirect, through the agency of fire. A careful study of the growth-forms of the grasses, with reference to the principle underlying Raunkiaer's system of classification, throws a good deal of light on the subject. *Aristida junciformis* and other coarse, wiry species oust the more valuable fodder species, such as *Anthistiria imberbis*, with the result that, from the farmer's standpoint, the veld deteriorates. That the change is due to the burning of the grass is shown by the fact that it is greatest along the railway, where the grass is always burned early in the year. The resulting "secondary" associations of Aristida, etc., are perfectly stable. *Anthistiria* is a Chamaephyte, *Aristida* a Hemicryptophyte. *Anthistiria* has the innovation shoots intravaginal, protected by the sheathing bases of the leaves. When the plant is burned, the fire may not only consume the withered leaves, but may also injure the innovation buds. If this does not happen, the buds, as a result of the fire, appear to be stimulated to grow, especially if the burning is done early, before the end of the rainy season. When winter comes the young stems are apt to be killed by the frosts and winter drought. *Aristida junciformis*, on the other hand, has the innovation shoots extravaginal, and sometimes it is stoloniferous. The innovation buds are protected by scales. This grass further grows in dense tussocks, and soil collects around and between the bases of the culms. When the veld grasses are burned—(1) the innovation buds of this species, being under the surface of the soil, are not liable to be injured by the fire, and (2) new growth does not take place so quickly, so that injury from frost and drought does not follow.

Those two species have been selected because each is the commonest example of its type. The other grasses resemble one or the other.

The Hemicryptophytes, with their innovation buds, extravaginal or at any rate below the level of the surface of the ground, are better adapted to withstanding grass fires, and hence, owing to the influence of these fires, are tending to oust the Chamaephytes, where the renewal buds are less efficiently protected. At the same time it must be remembered that *Anthistiria*, a typical Chamaephyte, is dominant in natural, unchanged veld. It must be assumed that but for grass fires the protection afforded the young buds by the sheathing leaves and layer of decaying foliage is quite efficient, and the fact that new growth can take place quickly in spring must be an advantage to the species in the absence of the disturbing factor, fire.

The above illustrates how a careful study of the autecology of a species very often affords an easy solution to questions of economic importance. To counteract the "deterioration" in the veld farmers should cease burning the grass.

GEOPHYTES.

In this class we have the greatest amount of protection during winter of all perennial plants, the renewal buds being deeply embedded in the soil. The subterranean portions are bulbs, tubers, corms, rhizomes, root buds and root tubers, and these contain a storage of food which enables the plant to flower early in spring—as a rule, before the work of assimilation is renewed. This is an abundant class in South Africa, including all our various bulbous monocotyledons. As in the case of the last class, the Geophytes of Natal are mostly veld plants, and the type resembles, in some respects, the floor vegetation of deciduous woodland in colder, temperate regions. The majority of the bulbous veld plants (Geophytes) are able to get their flowering over before the grass grows tall enough to shade them, in the same way as bulbous woodland plants in deciduous woods flower before the leaf canopy appears on the trees. Being, for the most part, deeply rooted, they occupy a different stratum of the soil from the grasses.

Geophytes, according to Raunkiaer's "normal spectrum," only form 3 per cent. of the world's flora as a whole. In Natal the proportion is about 18 per cent., or six times the normal, so that this must be considered quite a characteristic South African type. Their great abundance depends partly on the same conditions as we have seen have led to an increase in the number of Chamaephytes and Hemicryptophytes—the need for protection against drought, etc., in winter—partly on the further need for producing seed early in spring, before the Chamaephytes and Hemicryptophytes (grasses) grow tall enough to shade them.

The Geophytes share their habitat with the Hemicryptophytes, both being mostly veld plants. The H. class is below the normal, according to Raunkiaer's normal spectum. The percentage is 18 instead of 27 (see table on p. 632). But if we combine the two classes, which we are justified in doing, seeing that they are alike in so many respects, we get for Natal 18 + 18, or 36 per cent. of H. and G; for the world, as a whole, 27 + 3, or 30 per cent. of H. and G. The increase in the number of Geophytes in Natal may, therefore, be considered to have taken place at the expense of the Hemicryptophytes. When we take the two together, we get a higher percentage than the normal (36 per cent. as against 30 per cent.).

The total number of Geophytes is *cir.* 550, including 120 Asclepiadaceae, 135 Orchidaceae, 49 Irideae, 58 Amaryllidaceae, 150 Liliaceae, all except 38, therefore, belonging to these five families.

In the Asclepiadaceae we get either a tuberous "rootstock," which in some species (*e.g. Raphionacme*) is very large, or a cluster of tuberous roots. Many of the climbing species included in the lists of Phanerophytes also have tubers. The family, as a whole, has a milky latex.

In the Orchidaceae the species included in the above list are the terrestrial orchids, with tubers usually ovoid or globose, sometimes lobed. The bulk of the Natal orchids are terrestrial (for the Epiphytes *vide* p. 631).

In the Irideae we usually get a corm, as in species of *Moraea*, *Tritonia*, *Watsonia*, *Gladiolus*, *Homeria miniata*, etc., but sometimes a short, creeping rhizome, *e.g.* in *Moraea iridioides*.

A number of Irideae have no tuberous underground organs, and are included among Hemicryptophytes.

In the Amaryllidaceae we get a corm in *Hypoxis spp.*, and *Curculigo;* a bulb in the others.

In the Liliaceae the rootstock is tuberous in *Eriospermum* and *Tulbagia;* rootstock obscure in *Anthericum;* rootstock small, roots wiry or fleshy in *Chlorophytum;* and in the other genera we get a tunicated bulb, which is the favourite storage organ in this family.

The Aroideae (*Richardia*) have thick, fleshy rhizomes.

Oxalis has tuberous roots.

Geophytes may naturally be subdivided on the basis of the various types of storage organ, and each type is well represented in Natal, as has just been shown.

It is interesting also to note that certain species of *Dioscorea, Asparagus, Smilax, Behnia,* and various Asclepiads are climbing Phanerophytes, and, at the same time, Geophytes. This is, of course, a different thing from the case of species such as *Hebenstreitia,* etc., which sometimes occur as Chamaephytes or Hemicryptophytes, and, given other conditions, occur as Therophytes (Annuals).

If, as indicated above, we group together the Hemicryptophytes and Geophytes, we find that no fewer than 800 species of these belong to the seven natural orders—Compositae, Gramineae, Asclepiadaceae, Orchidaceae, Liliaceae, Amaryllidaceae, Irideae; and these all occupy the same habitat—the veld—and most of them flower about the same time.

The extraordinary profusion of flowers in the veld in early spring, and especially of representatives of those natural orders, is a fact which is never forgotten by the botanist who has once seen it. Not only is the number of species large, but many of them are found all over the country, and the type must be held to constitute a very important part of the vegetation of Natal.

HELOPHYTES.

Helophytes, or marsh plants, occur in the numerous Vleis. As has been shown in former papers, the Vleis of Natal can be graded according to (1) the amount of water; (2) the degree of stagnation of the water. There are also all gradations between veld and vlei, and certain species—*e.g.* Tambootie grass (*Andropogon nardus* var. *marginatus*)—occur either in veld or vlei. It therefore becomes a matter of some difficulty to determine which of such intermediate species are to be assigned to the present class, and which to the class already dealt with.

The Cyperaceae are, on the whole, mostly vlei plants, but a number—included above among the Hemicryptophytes—grow in the veld.

The class, Helophytes, it must be remembered, does not include all the so-called marsh plants. Some of the marsh Cyperaceae are annuals (Therophytes), and other plants which are typically found in the vleis are shrubs (Phanerophytes) or bulbous Monocotyledons (Geophytes). The class, Helophytes, is composed of perennial marsh plants, usually with creeping rhizomes, which have their renewal buds in the mud.

The total number of Helophytes is *cir.* 143 (including 81 Cyperaceae). Of these only 26 are Dicotyledons. There is no necessity in such a uniform and small class for any further subdivision. The bulk of them are sedges.

HYDROPHYTES.

These are the purely aquatic forms, and they are included by Raunkiaer with the Helophytes, the two together forming the class H.H. In Natal, Hydrophytes are scarce. There are no lakes of any size, owing to the steep rise of the land from the sea to the Drakensberg. In the dry winter season, in most districts, there are few pools of water even. The Hydrophytes, therefore, are mainly stream plants, but they are nowhere abundant.

The total number of Hydrophytes is 25. The total number of Helohydrophytes (Class H.H.) is *cir.* 168.

Raunkiaer gives 1 per cent. as the normal amount of H.H. This number seems to the writer to be too low. At any rate, in Natal it is at least five times that amount—5 per cent.

This higher proportion of marsh plants might be taken to indicate that much of the land in Natal is marshy. This is not the case. Vleis are exceedingly numerous, but not, as a rule, very large. The arrangement of successive terrace plateaux, with the rivers eating their way back through them, and with the general rate of denudation exceedingly rapid, leads to a network of small streams. These, wherever the ground is more or less flat, spread themselves out and form vleis. Consequently we have vleis at all altitudes and under every different kind of external condition known in Natal. Though, in spite of this, there is more uniformity in the vlei vegetation than in any other plant formation in Natal, yet the total number of vlei species (Helophytes) is greater than if the same total area of vlei had been confined, say, to the lowlying coast lands.

The high proportion of Helophytes therefore does not mean that a large proportion of the total area is marsh, but that there is a greater diversity than usual in the types of marsh.

THEROPHYTES.

These are the plants of the favourable season, the annuals. In temperate regions, Aestival or Summer Annuals, and Hibernal or Winter Annuals are distinguished. In Natal this distinction is not necessary, since they are all summer annuals. The vegetative period varies from one to several months. Therophytes are not numerous in Natal, the percentage being only one-half that of Raunkiaer's normal spectrum. A high percentage of Therophytes is characteristic—(1) of desert regions, particularly regions with dry, hot summers; and (2) of localities where the soil is regularly and periodically disturbed (cultivated land, sea-shore, sand, etc.). The Natal Therophytes belong mostly to the latter class, being the weeds of cultivated land. Many of them are exotic or doubtfully native of Natal.

It has been pointed out by the writer elsewhere (1, 2) that when cultivated land is allowed to revert to veld, the annual species are gradually replaced by perennials.

The total number of Therophytes is *cir.* 197, including thirty-six species of grasses. Several species here classed as annuals also occur as perennials while certain species classed as perennials always flower the first year and may be annuals.

Since the majority of the annuals which do occur in Natal are, as already mentioned, the weeds of cultivated land, and a high proportion of them are exotic, the climate of Natal is obviously not a Therophytic one. Though the drought is severe in winter, there is plenty of rain in summer.

The comparative scarcity of Therophytes must therefore be put down to two causes:

(1) The fact that Natal is not a country under high cultivation. The small area under mealies, etc., is out of all proportion to the vast stretches of virgin veld. It is true that a good deal of land is now being planted with Wattle (*Acacia mollissima*), but in the Wattle plantations weeds and all kinds of undergrowth are very scarce.

(2) The fact that Natal is a region of summer rainfall. On the west and south-west side of South Africa the rainfall is in winter, and the summers are dry. Annuals are undoubtedly more abundant there. An analysis of the flora of South Africa, as a whole, would show a higher percentage of annuals. Though the writer is not in a position to put forward such an analysis, there are plenty of facts to support this statement. For instance, 27 species of *Senecio* were included in the class "Annui" by Harvey in vol. iii of the *Flora Capensis*. That was published in 1864, and now the list might be extended.

In Natal, though *Senecio* is one of our largest genera (*cir.* 80 species and varieties) only one or two are annuals, and not one of Harvey's original 27 is recorded for Natal. Again, *Phyllopodium* has 18 South African species, of which 12 are annuals. Only one of the 12 belongs to Natal. Examples might be multiplied.

The hot, dry summers of the western portion of South Africa give a Therophytic climate which contrasts strongly with the eastern side.

The classes of growth-forms described so far form a fairly definite series from Phanerophytes to Therophytes, showing increased protection for the renewal buds during the adverse season. There are certain smaller classes of growth-forms which do not come into the series. Of these, Raunkiaer included two—the Stem Succulents and Epiphytes. A third is here added—the Heterophytes.

STEM SUCCULENTS.

These belong to a very few genera in the family Asclepiadaceae, viz.: *Caralluma lutea* (stems $1\frac{1}{2}$–4 in.), *Stapelia gigantea*, and *Stapelia woodii*, *Huernia hystrix*, *Sarcostemma viminale*, *Cynanchum sarcostemmatoides*, and about 23 species of *Euphorbia*.

The total number of Stem Succulents is therefore *cir.* 30.

The genus *Euphorbia* is very well represented in Natal and is one of the most heterogeneous in its growth-forms. It includes common field weeds and large trees, *e.g.* *E. tirucalli* and *E. grandidens*. The tree Euphorbias are very abundant in the dry river valleys and rocky hillsides of the Low Veld region. The Euphorbiaceae have not yet been dealt with in the *Flora Capensis*.

All stem succulents, like the other members of the families to which they belong, have a milky latex. This distinguishes the African forms from the similar "Cactoid" forms of America. The latex in both Euphorbias and Asclepiads is contained in the coenocytic type of laticiferous element. The readiness with which it flows shows that in most cases it is under high pressure in the plant.

EPIPHYTES.

If we restrict ourselves to the seed-bearing plants, the Epiphytes of Natal are about equal in number to the Stem Succulents. A large number of Pteridophyta and Bryophyta might, however, be added.

The total number of Epiphytes is *cir.* 34, the bulk of them being Orchids. They are not particularly abundant individually. The species *Rhipsalis cassytha*, our only representative of the family Cactaceae, is a fleshy, cord-like plant hanging from trees, but often found also on rocks. Hence it might have been included among Stem Succulents.

Dermatobotrys saundersii (Scroph.), a recently discovered species of *Cyrtanthus* (*C. epiphyticus* J. M. Wood), and two species of *Peperomia*, with *cir.* 30 species of Orchids belonging to the genera *Polystachya*, *Angraecum*, and *Mystacidium*, complete the list. *Ficus natalensis* begins its life as an epiphyte.

HETEROPHYTES.

These, though a small group, formed one of Warming's six main classes, and rightly so, for they differ from all other growth-forms among flowering plants.

In Natal we have the following: *Cuscuta* (4 species) and *Cassytha capensis* (holo-parasitic stem parasites), *Loranthus* (5 species), *Viscum* (8 species) (hemi-parasitic stem parasites).

The following Scrophulariaceae: *Melasma* (6 species), *Striga* (6 species), *Cycnium* (3 species), *Rhamphicarpa* (2 species), *Harveya* (5 species) (hemi-parasitic root parasites).

A few orchids are saprophytic or nearly so.

The total number of Heterophytes is *cir.* 40. The total number of species dealt with (including Heterophytes) is *cir.* 3074.

Since Heterophytes were not included by Raunkiaer as a separate class, we may neglect these and reckon, for statistical purposes, the total number of species included in the analysis as being 3034, distributed as follows:

	S.	E.	M.M.	M.	N.	Ch.	H.	G.	H.H.	Th.
Total number belonging to each growth form	30	34	95	420	430	570	540	550	168	197
Per cent. belonging to each form	1	1	3	14	14	19	18	18	5·5	6·5

The following table is taken from the paper on Raunkiaer's "Life-forms and Statistical Methods," by W. G. Smith, *Journal of Ecology*, vol. i, No. 1, and the results obtained for Natal are included in it for purposes of comparison:

Examples of Biological Spectra.

	Total number of species.	Percentage of species belonging to each life form.									
		S.	E.	M.M.	M.	N.	Ch.	H.	G.	H.H	Th.
Normal spectrum	400	1	3	6	17	20	9	27	3	1	13
Eastern N. America:											
Baffin's Land	129	—	—	—	—	1	30	51	13	3	2
Labrador coast	246	—	—	2	1	8	17	52	9	5	6
Georgia	717	0·1	0·4	5	7	11	4	55	4	6	8
Danish West Indies	904	2	1	5	23	30	12	9	3	1	14
Western N. America:											
St. Lawrence (Alaska)	126	—	—	—	—	—	23	61	11	4	1
Sitka	222	—	—	3	3	5	7	60	10	7	5
Death Valley	294	3	—	—	2	21	7	18	2	5	42
Western Europe, etc.:											
Francis Joseph Land	25	—	—	—	—	—	32	60	8	—	—
Spitzbergen	110	—	—	—	—	1	22	60	13	2	2
Iceland	329	—	—	—	—	2	13	54	10	10	11
Denmark	1084	—	0·1	1	3	3	3	50	11	11	18
Stuttgart	862	—	—	3	3	3	3	54	10	7	17
Madeira lowlands	213	—	—	—	1	14	7	24	—	3	51
Libyan Desert (Egypt)	194	—	—	—	3	9	21	20	4	1	42
Aden	176	1	—	—	7	26	27	19	3	—	17
Seychelles	258	1	3	10	23	24	6	12	3	2	16
NATAL	**3034**	**1**	**1**	**3**	**14**	**14**	**19**	**18**	**18**	**5·5**	**6·5**

The normal spectrum is given by Raunkiaer as approximately that of the whole world's flora. It was obtained by computation and checked in various ways. The other spectra must be judged by the amount of variation from the normal in each of the separate life-forms, and not by the highest percentage of each. Raunkiaer's statistics refer only to the Northern Hemisphere. He uses them to establish certain regional climatic zones, for a full explanation of which Smith's paper may be consulted (22). It is unfortunate that no statistics are available for the Southern Hemisphere. No climate zone can as yet be established here, but from the above table certain general conclusions can be drawn which apply to Natal as to other countries.

If the optimum point of the Biological spectrum is toward the left—*i.e.* in the groups M.M. and M.—it means that we have a favourable type of climate for tree growth—*i.e.* a Phanerophytic climate. A shifting of the optimum point to the right means increasing drought or other adverse conditions (frosts, etc.), particularly at one season of the year. We thus pass first to a Chamaephytic and then to a Hemicryptophytic type of climate. Still more severe conditions, dry summers, or general drought leads to a desert type or Therophytic type, the Therophytes being very abundant. The application of this Therophyte test enabled Ove Paulsen (18) to class the Transcaspian lowlands as desert rather than steppe. The Therophytes also increase in more highly cultivated areas—*e.g.* Denmark, Stuttgart.

GENERAL SUMMARY AND CONCLUSIONS.

The analysis of the flora shows that in Natal we have every type of life-form represented, indicating a rich and varied flora and corresponding variation in the environmental conditions. The same thing is shown by the large total number of species, 3074 (which does not include quite all the known species), and also by the variability seen in the growth-forms of the same species, especially among the Phanerophytes. The Megaphanerophytes are few in number and the Mesophanerophytes also fall below the normal, the class M. M. being 3 per cent. in Natal as compared with 6 per cent. in the normal spectrum. Tall trees are therefore not characteristic of Natal. Microphanerophytes (trees and shrubs below 8 metres) reach 14 per cent. as compared with 17 per cent., and Nanophanerophytes (shrubs under 2 metres) are 14 per cent. as compared with 20 per cent. in the normal spectrum.

Taking the Phanerophytes as a whole we see that they fall considerably below the normal, 31 per cent. instead of 43 per cent.

Seychelles, with a typical Phanerophytic climate, has 57 per cent. Phanerophytes, Danish West Indies 58 per cent. On the other hand, Natal has many more than the temperate regions of the Northern Hemisphere. Denmark has only 7 per cent., Stuttgart 10 per cent. Aden approaches nearest to Natal, but it has no Mesophanerophytes. All its trees are below 8 metres.

The presence of 1 per cent. of Epiphytes is interesting. The normal is 3 per cent., the same as Seychelles. Epiphytes are confined practically to countries with some degree of a Phanerophytic climate. The Danish West Indies also has 1 per cent., the same as Natal.

Natal does possess a Phanerophytic climate—in parts. The trees have to contend with adverse factors generally, but in certain situations these are lessened; or, to put it otherwise, a Phanerophytic climate is not general in Natal. Forests are confined to the south-eastern slopes of the hills, and in other plant-formations trees occur but grow isolated—*e.g.* in the Thorn Veld.

In the forests a very large number of species of Phanerophytes grow intermingled. There is not the same uniformity and marked dominance of one or two species that is found in the forests of the Northern Hemisphere. Considering how much more extensive the veld is than the bush in Natal, it is surprising to find that the percentage of Phanerophytes is so great as it is. The individual species show great plasticity and consequently great variation, according to differences in environmental conditions. In the larger classes the species may be arranged in a series showing increased xeromorphy. There must be taken into consideration, not only the effect of the non-living environment, but also the influence of one part of the vegetation on the rest. The Phanerophytes thus not only influence one another (and one class of Phanerophytes another class), but also other distinct classes. A considerable number of Chamaephytes are present in the bush, and owe their existence there to the presence of the Phanerophytes.

Hemicryptophytes and Geophytes, on the other hand, are not abundant in the evergreen bush of Natal as they are in deciduous woodland elsewhere. There is a large number of lianes among Natal Phanerophytes.

Considering next the three classes Ch., H., and G., we find that the percentages for Natal are respectively 19, 18, 18 as compared with 9, 27, and 3 in the normal spectrum. The climate of Natal to a great extent favours the greater protection of renewal buds, and therefore a much greater area is occupied by veld formation made up of those classes of growth-forms.

The grasses are either Ch. or H., but the present tendency is for the latter to oust the former. The high proportion of G. is explained when we take into consideration the fact that this type is best suited for association with the grasses in the veld owing to the necessity for early flowering, etc., as well as protection during winter, and, being more deeply situated in the soil, they do not directly compete with the grasses. The increase in the number of Geophytes corresponds to a decrease in the number of Hemicryptophytes. They are both veld types.

The number of Chamaephytes has been increased by the inclusion of species which depend on the presence of Phanerophytes, as explained above. The high percentage of Chamaephytes also shows the effect of drought. Aden, it will be seen, shows a similar effect. If the temperature were lower in winter there would be fewer Chamaephytes and more Hemicryptophytes, as shown by the figures for colder, temperate regions. Denmark, for instance, has only 3 per cent. Ch. and 50 per cent. H.

That this is not explained by the Chamaephytes being increased by the presence of Phanerophytes, is shown by the figures for Seychelles, which has a more Phanerophytic climate than that of Natal. They are 6 per cent. Ch. and 12 per cent. H.

The climate of Natal may be looked upon as mainly Chamaephytic, but not pronouncedly so. The high percentage of Geophytes (six times the normal) is so characteristic of Natal (and of South Africa as a whole), that this might be called the country of Geophytes.

The class, H.H., as will be seen from the table, varies greatly in different countries. In Natal we have 5·5 per cent., which seems to be about an average, though Raunkiaer gives 1 per cent. as the normal, a figure which is surely too low. This class of growth form composes the vlei formation of Natal. Vleis are very numerous at all altitudes, but nowhere very large. There are no lakes.

Therophytes in Natal are not very abundant. The percentage is 6·5, or exactly half the normal. Natal is certainly far removed from the desert type, and it is not under high cultivation. Probably the west side of South Africa has a much higher percentage of Therophytes, owing to the much more arid conditions prevailing there.

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